

being subject to the transformation). Again for an explicit solution of our problem we assume $\Phi[C/M]$ to be of the form

$$\Phi[C/M] = \varphi^{(0)}(M) + \sum_{i=1}^{\infty} \frac{1}{i!} \int_6 \int_6 \dots \int_6 \varphi^{(i)}(M, M_1, \dots, M_i) d\epsilon_1 \dots d\epsilon_i. \quad (9)$$

Then by a functional analysis similar to the one used for functionals of type (4), we can readily prove corresponding theorems to Theorem I and Theorem II.

The invariant theory of functionals of closed plane curves of types (4) and (9) can be generalized to functionals of closed spreads of $n-1$ dimensions embedded in the space of n dimensions. The reasoning involved in these generalizations is an obvious extension of the reasoning in the cases discussed in this abstract.

¹ The writing of this paper was suggested by Prof. G. C. Evans. Detailed proofs will be found in a paper to be offered to the *Transactions of the American Mathematical Society*.

² See papers by I. A. Barnett in these PROCEEDINGS, 6, 1920, 200 and in *Amer. J. Math.*, 45, number 1, Jan., 1923, 42; and also papers by the author in *Bull. Amer. Math. Soc.*, 30, number 7, July, 1924, 338 and in forthcoming issues of *Ann. Math. Princeton*, and the *Bull. Amer. Math. Soc.*.

³ From one point of view the classical theories of integral invariants may be considered as a first chapter in this invariant theory.

⁴ There is no loss of generality in making this assumption.

⁵ H. Poincaré, *Méthodes Nouvelles De La Mécanique Céleste*, Vol. III, p. 41.

RESIN CANALS IN THE EVOLUTION OF THE CONIFERS¹

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An outstanding characteristic of the Conifers as a group is the presence of canals producing turpentine and resin. These are present in the soft tissues or the wood in all Conifers with the sole exception of the genus *Taxus*. Since they are so universal a feature of organization, in this large and ancient group of plants, their evolutionary history has naturally been the subject of much discussion. The view generally held, at the present time, is that those Conifers in which the system of resin canals is most strongly developed, namely the Abietineae, represent the most modern and specialized forms. The geological history of Conifers, however, scarcely warrants such a conclusion however much it may harmonize with a purely philosophical interpretation of evolution as proceeding from the simple to

the more complex. Our knowledge of ancient groups of plants makes it tolerably clear, that in those forms, which are no longer dominant in our Earth's flora, the more complicated forms lie in the past rather than in the present. The Conifers are a group to which this general principle strikingly applies for they had their greatest development in the Mesozoic age.

In the living pine and its prototypes, in the Mesozoic, resin canals are present both vertically and horizontally, and form a continuous system in wood and bark, which is commonly tapped for turpentine and resin. In the higher members of the pine family, the hemlock and the fir, these canals disappear in the wood but are still prominent in the soft tissues. An interesting fact, in this connection, is that resin canals are always present in the wood of the root in the higher Abietineae. Another interesting situation which has been developed by the present author, is the occurrence of resin canals as a consequence of injury. This phenomenon has been shown to be present by the author in the four genera *Tsuga* (the hemlock), *Abies* (the fir), *Pseudolarix* (the golden larch of China) and *Cedrus* (the cedar of Lebanon, the Deodar, etc.). The cedar of Lebanon, and other species of the genus, are characterized by the occurrence of both vertical and horizontal resin canals following injury. In the other genera cited above, only vertical canals result in living species from injury. It is of interest, in this connection, to note that *Cedrus* has the oldest geological record of any of the four genera occurring as it does, in the Argonne in France, in the Cretaceous cliffs of the south of England, and in our own Potomac formation. A very interesting fact has developed in the case of the genus *Abies* from the American Miocene. Some years ago, the present author described a wounded wood, which was excavated in the construction of a tunnel, through the Sierra Nevada mountains, underneath sixty feet of conglomerate. This extinct form was characterized by resin canals, both in the horizontal and vertical planes. A figure of this interesting and important specimen is herewith introduced. It will be seen by examining the photograph, fig. 1, that resin canals of a small size appear in transverse sections, while a larger one can be seen in horizontal section. It thus follows that the firs of earlier date gave a wound-reaction, more like that of the very ancient genus *Pinus*, than do the modern species of *Abies*.

Another interesting feature of living pines is the presence of horizontal tracheids accompanying the rays. These are absent in certain of the higher Abietineae, notably the firs, but may be recalled by injury precisely as is the case with the resin canals just described.

A large and important sub-tribe of Conifers is the Cupressineae, using that term in its broadest sense. In these, the seed-bearing cone shows a simpler structure than does that of the Abietineae and resin-canals are absent in the wood. Perhaps the most interesting and ancient of the Cupressineae, in the broad sense, is the genus *Sequoia*, which has as its

surviving representatives, the Big Tree and the Redwood, both occurring west of the Rocky Mountains. Some years ago, the author pointed out that the two surviving species of *Sequoia* are both characterized by wound resin canals, fig. 2. In the Big Tree, resin canals also occur normally in the first year's growth, fig. 2, apparently in harmony with the principle of recapitulation. It has been shown by investigations, in the author's laboratories and elsewhere, that marginal ray tracheids may be recalled, not only in *Sequoia*, but also in other genera of the Cupressineae. The most interesting feature of the wound-reaction of *Sequoia* is found, however, in its more ancient representatives. *Sequoia*, in the Tertiary, shows the same reaction to wounding as do the surviving genera. In the Laramie Cretaceous, however, it is clear from investigations carried on by Dr. R. E. Torrey that this genus,² which here makes its first authentic appear-



FIGURE 1

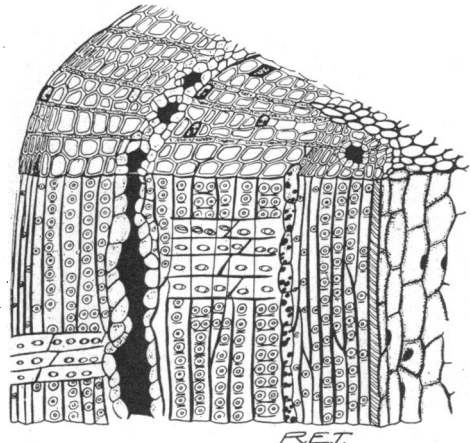


FIGURE 2

ance, is characterized in a number of species by traumatic resin in canals, both vertical and horizontal, fig. 3. In other words, the experimental evidence in the case of *Sequoia*, indicates clearly that it has come from pine-like ancestors and that in its more ancient representatives the resemblance to the pine in its wound responses, becomes more and more marked. The conclusion has been drawn by the present author, from these data, that the Cupressineae in a large sense are evolutionary derivatives of the pine.

Another very important sub-tribe of the conifers is the Araucariineae, a group at the present time confined to Australasia and South America, but formerly flourishing in very great abundance through the Northern Hemisphere. It is commonly assumed that the Araucarian Conifers are the most ancient and connect that group with Palaeozoic times. Anatomical and experimental investigations, however, are far from justifying any such conclusions. The present writer has described a number of Araucarian forms,

which have a wound-reaction like that of *Sequoia* and the firs, for resin canals make their appearance as a consequence of traumatic stimulation. This situation has been the subject of much discussion on the part of European investigators, who have questioned, without exception, the validity of the writer's conclusions. European palaeobotanists assume that the undoubted presence of wound resin canals in the case of supposed Araucarian Conifers removes them from the category of Araucariineae, and transfers them to the Abietineae. The writer and his students have established a number of genera of Araucarian woods of different types with Abietineous wound-reactions. The Europeans have recently transferred these wholly to the Abietineae, claiming that they represent a stage in the evolution of the Abietineae from Araucarian ancestors. Figure 4 shows a diagrammatic

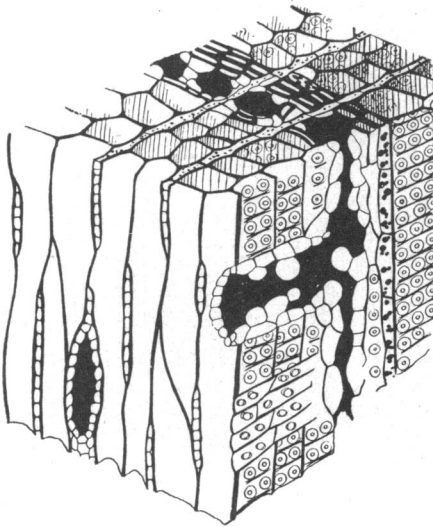


FIGURE 3

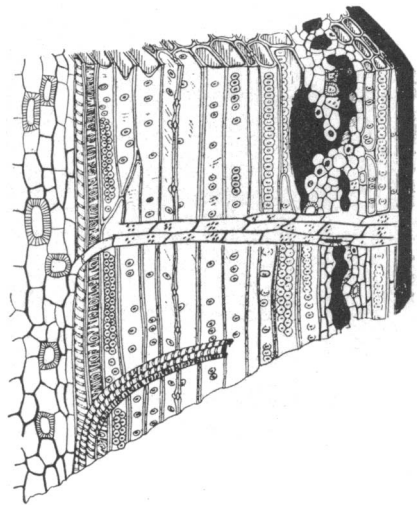


FIGURE 4

representation of the wounded wood of *Brachyoxylon*. The resin canals are represented as filled with black contents and obviously run only in the vertical direction.

Although the later Mesozoic woods with Araucarian structure and Abietineous wound-reactions have wound canals only in the vertical plane, those of lower geological range, namely, the Infracretaceous and Jurassic, have both vertical and horizontal wound canals, precisely as is the case with the older representatives of *Sequoia* and *Abies*. If logic prevails in this instance, we are compelled to conclude that the older Araucarian Conifers are nearer the Abietineae than the modern forms and that they are derived from the Abietineous stock. The European palaeobotanists conclude otherwise, and have recently transferred a host of woods formerly regarded

as undoubtedly Araucarian, from the Araucariineae to the Abietineae. As a result, we have a very interesting situation. The strongest argument for the antiquity of the Araucarian Conifers has been the supposed great abundance of their woods in the later Mesozoic. By the removal of practically all woods formerly regarded as Araucarian to the Abietineae, this argument becomes without force.

The general situation is of considerable interest. The higher Abietineae, the lower Cupressineae, and a large group of Conifers, until very recently unanimously considered to be Araucarian, all independently present wound-reactions indicating affinity with the very ancient genus *Pinus*. The logical conclusion is obviously to regard the higher Abietineae, the Cupressineae and the Araucariineae, all as offshoots of the Abietineae. If one adopts on the other hand, the view in vogue in Europe, one has to suppose not only that the higher Abietineae have produced the very ancient *Pinus*; but also that the Cupressineae have independently given rise to pine-like forms and finally that the same conclusion is to be adopted in the case of the Araucarian Conifers.

The only large group not considered in the above statement are the Taxads or yew-like Conifers, at present mainly confined to the Southern Hemisphere. The author is, at the present, endeavoring to secure material of these forms in the strata of their present seats. Should the experimental evidence in their case lead to the same conclusions as in the Abietineae, Cupressineae and Araucariineae, it will be scarcely possible for the European anatomists to continue to maintain their present illogical position. The resemblance of the lower Podocarps and Yews to the Abietineae is striking, even in their modern representatives, and the study of their fossil forms along experimental lines should prove of fundamental importance from the standpoint of the doctrine of descent.

¹ Investigation prosecuted with the aid of a grant from the Elizabeth Thompson Science Fund.

² The comparative Anatomy and Phylogeny of the Coniferales. Part 3.—Mesozoic and Tertiary Coniferous Woods, *Memoirs Boston Soc. Nat. Hist.*, 6, Number 2, April, 1923.